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ART. XXI.—*The Evolution of the Elephant* ;* by RICHARD S. LULL.

CONTENTS :

PART I.

THE modern word elephant, which may be used comprehensively to include all of the proboscidians, comes from the Greek ἐλέφας (ἐλεφαντ), a word first used in the literature by Herodotus, the father of history. The origin of the word is somewhat a matter of doubt, certain authorities deriving it from the Hebrew *eleph*, an ox; others from the Hebrew *ibāh*, Sanskrit *ibhas*, an elephant, comparing this with the Latin *ebur*, meaning ivory. Another Sanskrit word is *hastīn*, elephant, from *hasta*, a hand or trunk. Thus the ancients emphasized the three characteristics of the proboscidians, size, the tusks, and the trunk, which are the most striking features of the most remarkable of beasts.

The proboscidians may be defined as large, trunk-bearing mammals, with pillar-like limbs, short neck and huge head, often with protruding ivory tusks, the modified upper and, in earlier, extinct types, the lower incisor teeth. The proboscidians constitute a sub-order of the great group of ungulates or hoofed mammals, yet have their nearest living allies in creatures strangely remote in size, form and environment from the lordly elephant, for the paleontologist, in his ardent search for family trees other than his own, often discloses some seemingly paradoxical relationships which completely upset the older ideas of classification. Explorations have recently brought to light evidence to show that the sea-living Sirenia, whose American representative is the Florida manatee, can claim close relationship with the elephants, though nothing

* An earlier paper in the same series, on the Evolution of the Horse Family, was published in the number for March, 1907.

could be more unlike than the proboscidians and the fish-like Sirenia with broad swimming tail, front limbs reduced to flippers, and no hind limbs at all. On the other hand, anatomists had already recognized certain similarities of structure between the elephants and the *Hyracoidea*, the Hyraces, or conies, furry, rabbit-like animals not more than 18 inches in length, short ears, tailless, and with hoof-like nails instead of the claws one would be led to expect from their general

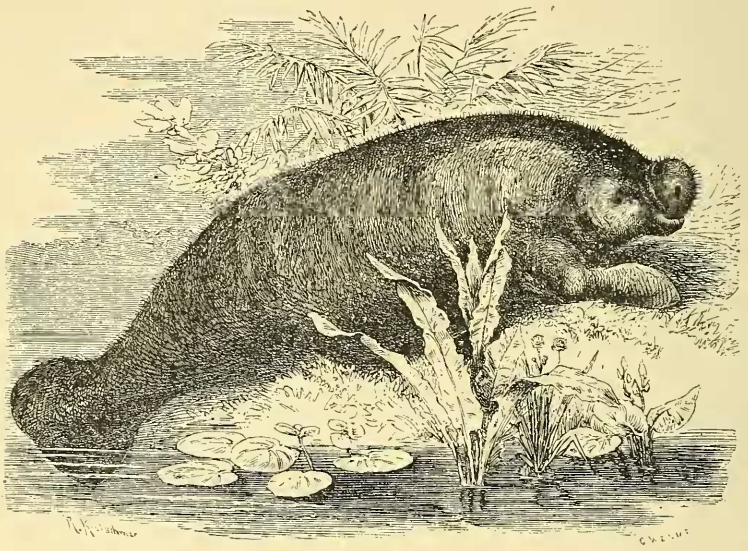

Fig. 1. The Manatee, *Manalus australis;* after Brehm.

appearance. They are confined to Africa with the exception of the Syrian conies, which the Book of Proverbs tells us "are but a feeble folk, yet make their houses in the rocks." Recent exploration in Egypt has revealed the presence of a hyrax much larger than the modern representatives of the order, and proclaiming by its structure a much closer approximation with the early elephants whose bones are found entombed in the same deposits.

Elephants show a curious intermingling of primitive and specialized characters, for in spite of the remarkable development of teeth, tusks, and trunk, many of the other bodily features would serve to place them among the most archaic of the ungulates.

The primitive features of the elephants, briefly enumerated, are as follows: simplicity of stomach, liver, and lungs and the

rather low type of brain. The limbs combine the archaic features of five toes in front and rear and a serial arrangement of wrist and ankle bones with the admirable adaptation of the entire limb to the support of the huge body. The limbs are further primitive in the retention of both bones of the lower leg and arm, for in most other ungulates one of these in each

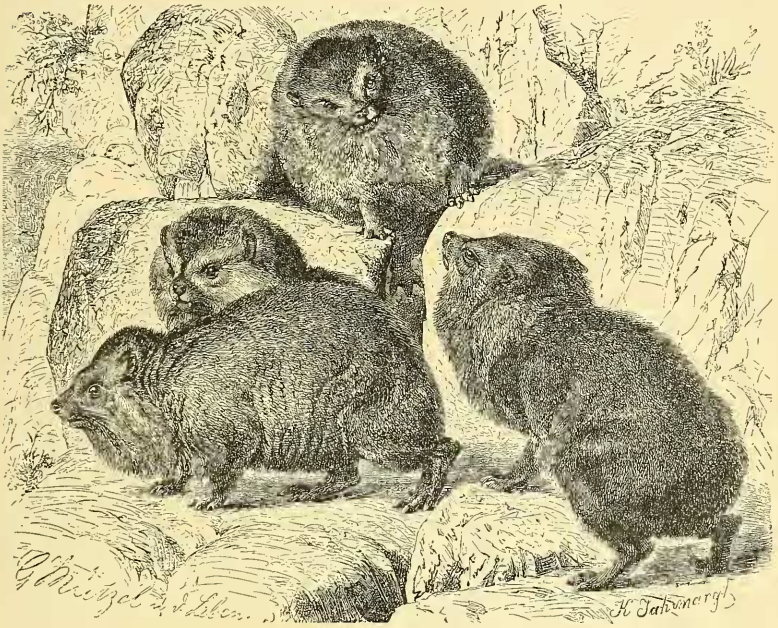

Fig. 2.—Conies, *Hyrax abyssinicus;* after Brehm.

member becomes greatly reduced, being, for part of the length at least, often entirely absent.

The special adaptations are, as in the horses, primarily for food-getting and locomotion, although incidentally the elephants have developed admirable weapons for defense, which, together with the great size and thick skin, render them almost impregnable to their enemies of the brute creation.

Adaptations of the Limbs and Feet.

The development of the pillar-like limb of the elephant has been shown to be merely a device to support the enormous bodily weight and was independently acquired in other groups of land animals of huge size. In most quadrupeds, however,

the knee and elbow are permanently bent, the upper limb-bones being of the shape of an elongated S. Increasing weight necessitates a straightening of the limb in order that the weight may be transmitted through a vertical shaft. This is more far-reaching than one would suppose, as it implies also a straightening of the bones themselves and a shifting of the articular facets from an oblique to a right angle with reference to the long axis of the bone. The foot has changed its posture

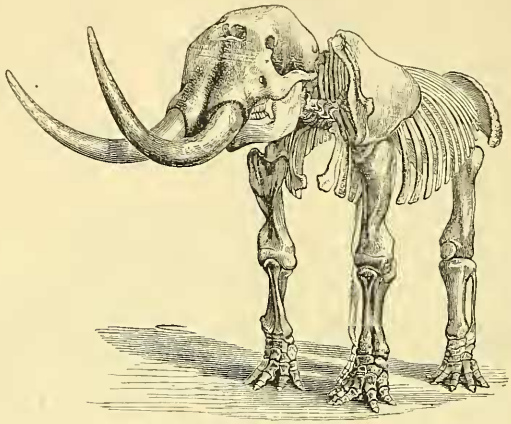

Fig. 3. American Mastodon; after Owen.

from the primitive plantigrade position, for the heel and wrist bones are elevated above the ground and a thick pad of gristle has developed beneath them in each foot, forming a cushion to receive a share of the weight. The toes are not separate but are imbedded in the common mass of the cylindrical foot, the hoofs being represented by nails around its forward margin. These may be fewer in number than the toes.

Adaptations of the Skull and Teeth.

Owing to the shortness of the neck and the height of the head from the ground, the proboscis or trunk, which is merely an elongation of the combined nose and upper lip, becomes a most necessary device for securing food and water. This organ is composed of a great number of muscles and so combined and controlled as to give not only enormous strength but the utmost delicacy of movement. The trunk terminates in one (Indian) or two (African elephant) finger-like projections, with which a pin can be picked up from the ground while the entire organ has sufficient strength to uproot a tree.

The development of the trunk has been accompanied by a marked change in the character and form of the skull, which is merely a mechanical adaptation to provide the leverage necessary to wield so weighty an organ. This has been brought about by a shortening of the skull accompanied by a corre sponding increase in height. The result is that the base of the trunk has been brought much nearer the fulcrum at the neck, thus shortening the weight arm of the lever, while the increasing height not only lengthens the power arm but gives more surface for the attachment of muscles and the great elastic *ligamentum nuchæ* which aids in supporting the head.

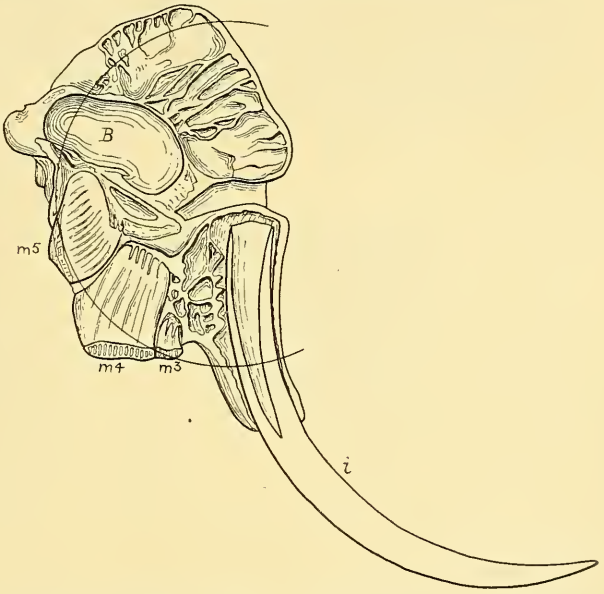

Fig. 4. Sectioned skull of Indian elephant; after Owen.

This change in the form of the skull, while it gives to the physiognomy of the animal that dignified, intellectual look, does not imply a similar development of the brain, for the brain case has increased but little, the great size of the skull being largely due to the development of air cells in the cranial bones so that the actual thickness of the roof of the skull is greater than the height of the brain chamber itself, a feature well shown in fig. 4.

The Teeth.

It is generally true among mammals that the normal number of teeth in the adult is forty-four, eleven in each half of

each jaw. This number is rarely exceeded, but often because of specialization a reduction in numbers occurs until, as in the ant-bears, the limit of a totally toothless condition may be reached. The elephants, owing to the great increase in the size of the individual grinders and the loss of all but two upper incisors in the forward part of the mouth, have the total number of teeth reduced *apparently* to six, as but one fully formed grinder is in use in each half of each jaw at any one time.

Actually, however, the number of teeth is greater than this, owing to the peculiar manner of tooth succession in which, instead of having the adult teeth replace those of the milk set vertically, the succession is from behind forward. The tooth forms in the rear of each jaw and moves forward through the arc of a circle (see fig. 4.), gradually replacing the preceding tooth as it wears away through use, until the final remnant is crowded from the jaw and the new tooth is in full service. Bearing this in mind, it is evident that the full tooth series is not confined to those present at any one time, but should include not only teeth which have gone before, but, in a young animal, those yet to come. Sir Richard Owen gives the total dentition of the modern elephant as follows:—incisors $\frac{2-2}{0-0}$, molars $\frac{6-6}{6-6}=28$, which being interpreted means that there are in each half of the upper jaw two tusks, the first milk tusk being succeeded by the permanent one, while in the lower jaw there are none. There are all told six grinders in each half of each jaw, the first appearing at the age of two weeks and being shed at the age of two years. The second is shed at the age of six, the third at nine, the fourth from twenty to twenty-five, the fifth at sixty, while the sixth lasts for the remainder of the creature's life, up to the age of a hundred to a hundred and twenty years.

The structure of a single tooth finds no exact parallel among other mammals, as it consists of a series of vertically placed transverse plates, each composed of a flattened mass of dentine or ivory surrounded by a layer of enamel. The plates are in turn bound together into a solid mass by a third material known as cement. When the upper surface of the tooth becomes worn through use, the hard enamel appears as a series of narrow transverse ridges between which lie the dentine and cement in alternate spaces, as two enamel ridges with the enclosed dentine are derived from each plate. In order to keep the teeth in proper condition a certain amount of harsh, siliceous grasses or woody material is necessary, otherwise the teeth become as smooth as polished marble and, as the rate of growth is nicely adjusted to normal wear, the elephant suffers

greatly when given improper food. The number of plates in the largest teeth varies from ten or eleven in the African elephant to twenty-seven in the Indian. The hairy mammoth had the most numerous and finest plates of all, representing in this respect the culmination of evolution.

The tusks are merely modified incisor teeth of the upper jaw which continue to grow throughout life. They are com-

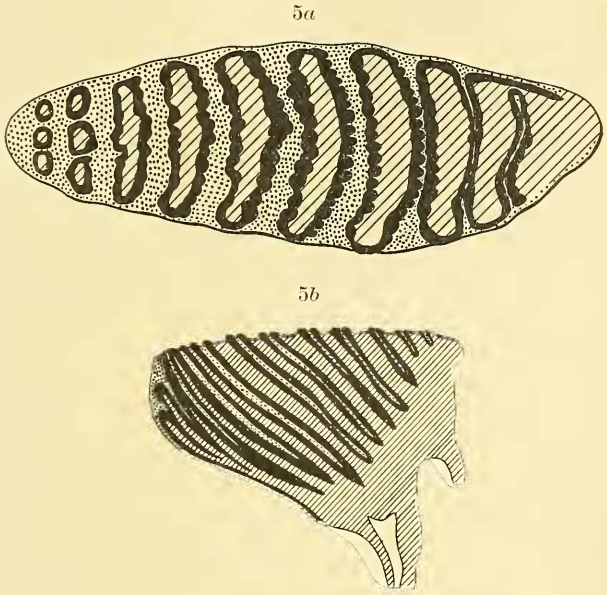

Fig. 5. Crown view and section of a molar tooth, original.

posed entirely of dentine or ivory of a superlative quality, the enamel being reduced to a small patch at the tip which soon becomes worn away. The tusks have various uses, but their primitive purpose is for digging. The African elephant is so industrious a digger that the right tusk is always the shorter, as it has to bear the brunt of the work. Tusks are so small as to be apparently absent in the female Indian elephant and often in the male, while they are present in both sexes in the African species. In size they are always much smaller in the Indian form, as seventy-six pounds is the maximum weight for a single tusk, while the greatest recorded size of those of the African elephant is 10 feet $\frac{3}{4}$ inches in length by 23 inches in circumference at the base, with a weight of 224 pounds for the right tusk, while the left measured 10 feet $3\frac{1}{2}$ inches in

length by 24½ inches in circumference and weighed 239 pounds, a total of 463 pounds for the pair!

Mentality.

In spite of its archaic type the brain is large and the surface is highly convoluted, the weight being on the average 8½ pounds; more than double that of man. The intelligence of the elephant has been exaggerated by some writers and greatly minimized by others. Sir Henry Baker, a British explorer, and the German naturalist Schillings, give us the most unbiased view of the mentality of the elephant. Elephants possess a remarkable memory of injuries, real or fancied; of misfortunes; and of the time and place of the ripening of favorite fruits. They also learn to perform complex labors, as the carrying and piling of logs in the teak yards in India without other directions than the initial order. They are said to be weather-wise and to be able to foretell rain some days in advance. Elephants are obedient and docile, notably those of India, but the males especially are subject to periods of nervous excitement, apparently of a sexual nature, known as "must," when they become very dangerous and sometimes destroy the keepers in their paroxysms of rage. Ultimately all male elephants become surly and intractable; in the wild state such are known as rogues and live apart from their kind until they die. A fine specimen of the Indian elephant known as "Chunee" was brought to England in 1810. He was very tractable and continued to grow until 1820, when the first paroxysm occurred, in which he attempted to kill his keeper. Similar paroxysms occurred with increasing force until 1826, when the violence of the animal necessitated its slaughter. With "Chunee" this condition occurred very early in life, as the animal was not fully adult at the time of its death. The famous "Jumbo," an African elephant, was sold from the London Zoölogical gardens because he was no longer trustworthy, from the same cause. He was not, however, a confirmed rogue, even when he died three and a half years later. Jumbo was about seventy-five years old at the time of his death.

There is a possible parallelism between human mental development and that of the elephant. One of the most potent factors in the evolution of man's mind is his ability to handle various objects and thus bring them before the face for examination. This is also found in the elephant, although to a less extent, and undoubtedly has aided materially in its mental development as well.

Elephants are rightly accused of timidity and cowardice, though, when brought to bay, rage may simulate courage,

making a charging tusker a most formidable foe. In common with most forest and jungle dwellers, elephants, while relatively dull of sight, are keen of scent and hearing, in fact marvelously so, for, as Schillings tells us, they either have an acuteness of some known sense far beyond our comprehension or possibly some other sense unknown to us. The sentinels of the herd stand with uplifted trunk, which emphasizes the value of the sense of smell.

Elephants rarely breed in captivity, almost all of the tamed individuals having been born wild; hence artificial selective breeding which has given rise to such valuable results in the betterment of domestic animals is unavailable for the improvement of the race.

The rate of increase is extremely slow, for Darwin tells us that they begin to bear young at thirty years and continue to do so until ninety, during which time six single young are produced on the average. But, to illustrate the necessity of a check upon increase among animals, Darwin says that even at this slow rate the offspring of a single pair would in 500 years amount to fifteen millions, provided they all lived to maturity!

Evidences of Evolution.

The evidences of evolution are threefold: structure, as shown by comparative anatomy, ontogeny or individual development, and phylogeny or racial history. The last paleontology makes known to us. We may, by comparing the structure of a given form with that of other animals, gain an insight into the probable course of modifications which it has undergone in the development of its distinctive features and often a hint at least as to its ancestry and relationship, as in the case already mentioned of the Hyracoidea and elephants. Again, the small hind-limb and hip bones buried deep within the body of the whales and the hip bones alone in the case of the manatee (Sirenia) having no possible function, are indubitable evidence for descent in each case from some land-dwelling quadrupedal type. This has been corroborated in the last instance by the recent finding, in the Eocene of the Egyptian Fayûm, of Sirenia *with* hind limbs.

Ontogeny.

Embryology shows us the curious parallelism which exists between the individual's history and that of the race, that of the individual being in most cases a more or less abridged summary of that of its ancestors.

I have spoken of the shortening and corresponding increase in height of the elephant's skull to provide the leverage

necessary in wielding the huge trunk. The development of this feature is beautifully shown in individual growth, for the new-born elephant has a relatively long, low skull the walls of which are slightly thickened so that the brain chamber fills the skull completely as in most other mammals. During the

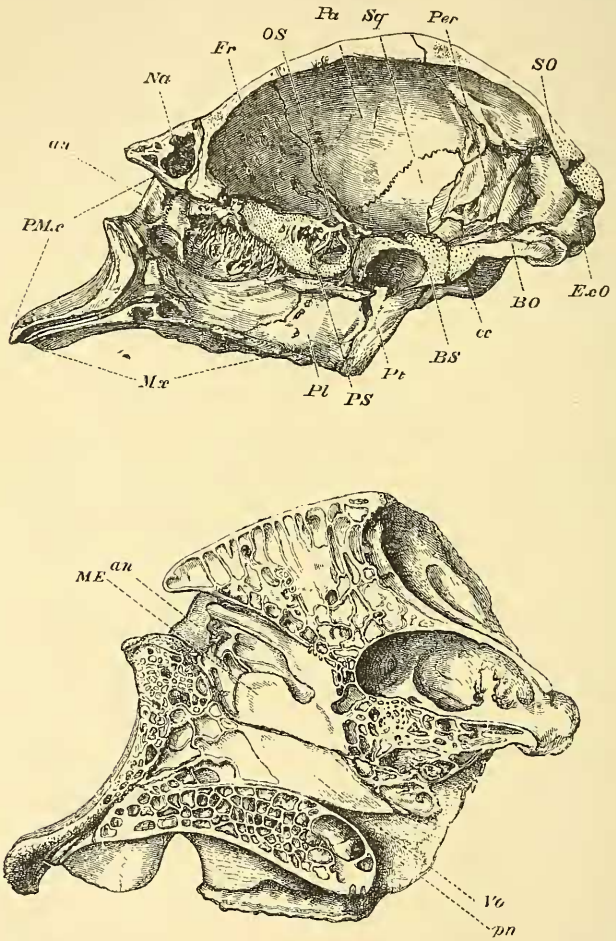

FIG. 6. Section of skull young ($\times \frac{1}{4}$), and old ($\times \frac{1}{12}$); from Flower's Osteology.

course of growth, however, the skull walls thicken greatly through the development of the air cells, while the brain cavity increases comparatively little, just as one would predict from the structure of the adult skull.

Of the prenatal life of the elephant, covering a period of twenty months, we know very little, but it is reasonable to suppose that embryology would give us much more light upon the development of elephantine features. New-born young are elephant-like in every particular with the exception of the skull.

Paleontology.

The great proof of the evolution of a race of animals is the finding in the ancient rocks more and more primitive forms as one recedes in time, until the most archaic type is reached. By the study of such a series of fossils not only may the evolutionary changes be learned, but former geographical distributions, the original home and the various migrations of the race. While this matter is treated much more fully in the second and third parts of this paper, a brief summary of the racial history may be given as follows:

The earliest known proboscidians were discovered in the Egyptian Fayûm, in beds of middle Eocene age. Their remains are also found in the Upper Eocene of the Fayûm, but the Oligocene elephants are as yet undiscovered. During the early Miocene the first migration occurred into Europe and thence to the region of India and even as far as North America, both of which were reached by the Middle Miocene. The Pliocene saw the elephants in their millenium, having reached the widest dispersal and the maximum in numbers of species. During Pleistocene times the Proboscidia covered all of the great land masses except Australia, but were diminishing in numbers, and toward the close of the Pleistocene the period of decadence began, resulting in the extinction of all but the Indian and African elephants of to-day.

Summary of the Evolution.

The physical changes undergone by the race are also clearly shown, as the paleontological series is very complete. These changes may thus be summarized: Increase in size and in the development of pillar-like limbs to support the enormous weight. Increase in size and complexity of the teeth and their consequent diminution in numbers and the development of the peculiar method of tooth succession. The loss of the canines and of all of the incisor teeth except the second pair in the upper and lower jaws and the development of these as tusks. The gradual elongation of the symphysis or union of the lower jaws to strengthen and support the lower tusks while digging, culminating in *Tetrabelodon angustidens*. The apparently sudden shortening of this symphysis following the loss of the lower tusks and the compensating increase in size and the change in curvature of those of the upper jaw.

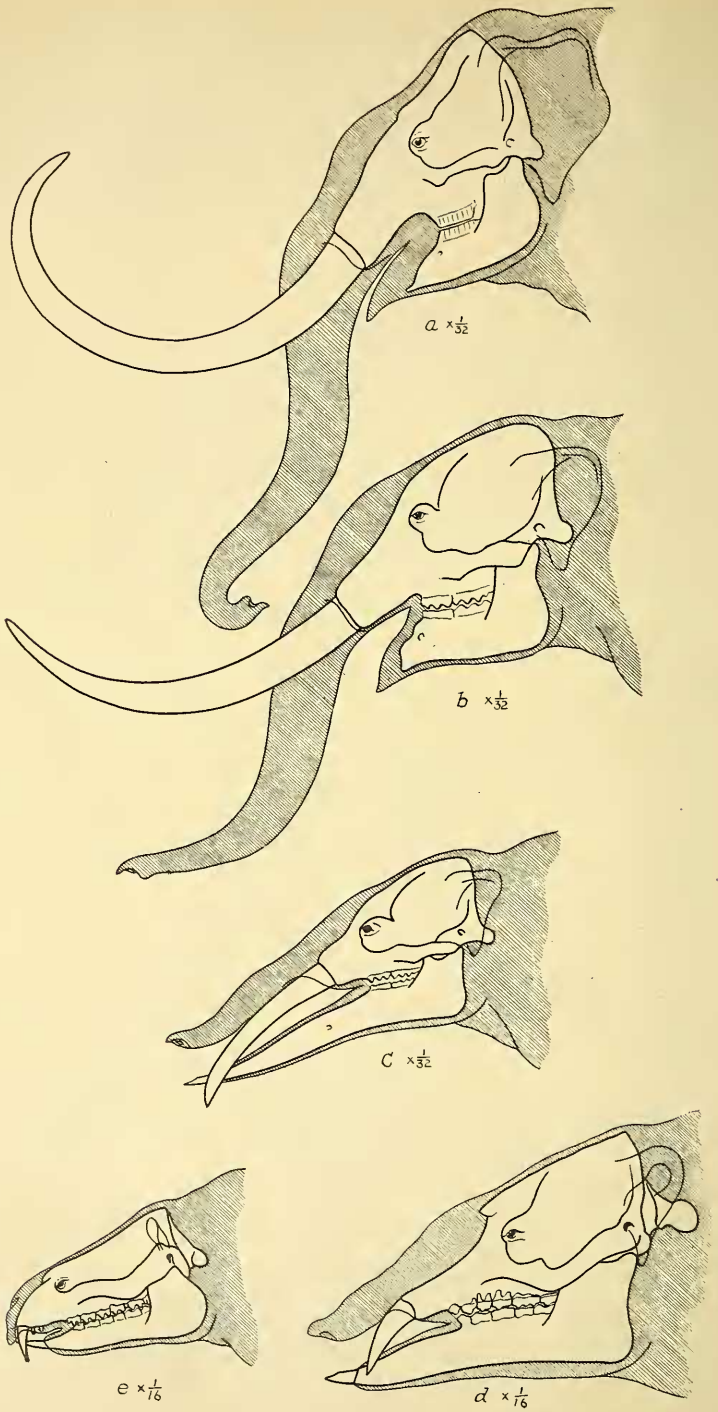

Fig. 7. Evolutionary changes of Proboscidia.

The increase in bulk and height, together with the shortening of the neck necessitated by the increasing weight of the head with its great battery of tusks, necessitated the development of a prehensile upper lip which gradually evolved into a proboscis for food-gathering. The elongation of the lower jaw implies a similar elongation of this proboscis in order that the latter may reach beyond the tusks. The trunk did not, however, reach maximum utility until the shortening jaw, removing the support from beneath, left it pendant as in the living elephant.

The change in the form of the skull developed *pari passu* with the growth of the tusks and trunk, as it is merely a mechanical adaptation to give greater leverage in the wielding these organs. It may readily be seen that these changes curiously interact upon one another; the result of the evolution of its parts being the development of a most marvelous whole.

Elephants Contemporary with Man.

Aside from the species of elephant now living, at least three extinct types were coeval with mankind, one distinctively American, the mastodon, *Mammut americanum*, one confined to Europe and southern Asia, *Elephas antiquus*, while the third, the hairy mammoth, *Elephas primigenius*, was common to both and to northern Asia as well. Of these the mammoth is without exception the best known of all prehistoric animals, for not only have its bones and teeth been found in immense numbers, but, in several instances, frozen carcasses have been discovered nearly or quite intact, the hair, hide, and even the viscera and muscles wonderfully preserved. In many instances these were irrevocably lost or were devoured by the dogs and wolves or by the natives themselves; two specimens have been preserved however and are now in the St. Petersburg zoölogical museum.

Of these one was found in the Lena Delta in Siberia in 1799 and secured in 1806. The skeleton with patches of hide adhering to the head and feet may still be seen, but the flesh of the animal was devoured by wolves and bears after being preserved in Nature's cold storage warehouse for thousands of years (see fig. 26). In 1901 another specimen was found at Beresovka, Siberia, 800 miles west of Behring strait and 60 miles within the arctic circle. It is supposed that this creature slipped into a crevasse in the ice which may have been covered by vegetation as in the Malaspina glacier of Alaska. That the poor brute died a violent death is certain from the fracture of the hip and one foreleg, and the presence of unswallowed grass between the teeth and upon the tongue. A great mass of clotted blood in the chest tells how suddenly the Reaper over-

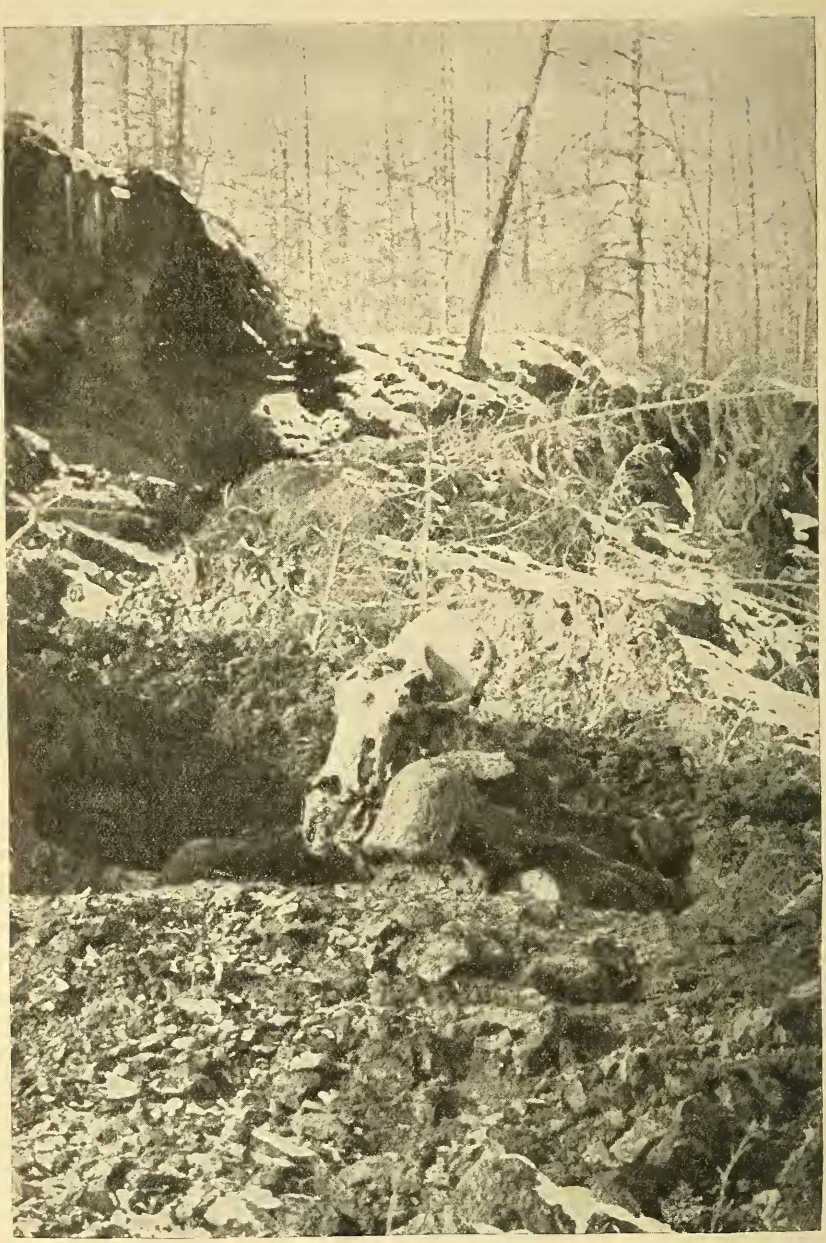

FIG. 8. Mammoth of 1901 *in situ*; after Herz.

took it, the creature having burst a blood vessel in its frantic efforts to extricate itself. Much of the hair had been destroyed when the animal was dug out of the cliff, but the collector, M. O. F. Herz, has preserved a very accurate record of texture and color of the hair on different parts of the body. This consists of a wooly undercoat, yellowish-brown in color, and an outer bristly coat, varying from fawn to dark brown and black. The hair on the chin and breast must have been at least half a yard in length and it was also long on the shoulders; that of the back, however, was not preserved.

This interesting relic is mounted in the St. Petersburg museum, the skin in the attitude in which it was found, while the skeleton is in walking posture beside it.

Immense quantities of fossil ivory have been exported from Siberia, there having been sold in the London market as many as 1,635 mammoth tusks in a single year, averaging 150 pounds in weight; of these but 14 per cent were of the best quality, 17 per cent inferior, while more than half were useless commercially. The total number of mammoths represented by the output of fossil ivory since the conquest of Siberia is not far from 40,000, not, of course, a single herd, but the accumulations of thousands of years. The oyster trawlers from the single village of Happisburg dredged from the Dogger Banks off the coast of Norfolk, England, 2,000 molar teeth, besides tusks and other mammoth remains, between the years 1820 and 1833. This indicates not only the great profusion of the mammoths of the Pleistocene, but the existence of comparatively recent land connection between England and the continent.

Direct evidences of the association of man and the mammoth are plentiful in Europe but strangely enough absolutely wanting in North America, although we have every reason to believe that such an association existed in the New World as well as in the Old. In Europe not only have the bones of man and the mammoth been found intermingled in a way that implied strict contemporaneity, but still more striking evidence is shown in the works of prehistoric artists. The fidelity with which the mammoth is drawn indicates that the artist must have seen the animal alive.

One of the most notable of these relics is an engraving of a charging mammoth drawn upon a fragment of mammoth tusk found in a cave dwelling at La Madeline in southern France. In the Grotte des Combarelles (Dordogne), France, there are in addition to some forty drawings of the horse at least fourteen of the mammoth. These are mural paintings or engravings, the former being executed in a black pigment and some kind of a red ochre, while the latter are scratched or deeply incised, sometimes embellished with a dark coloring

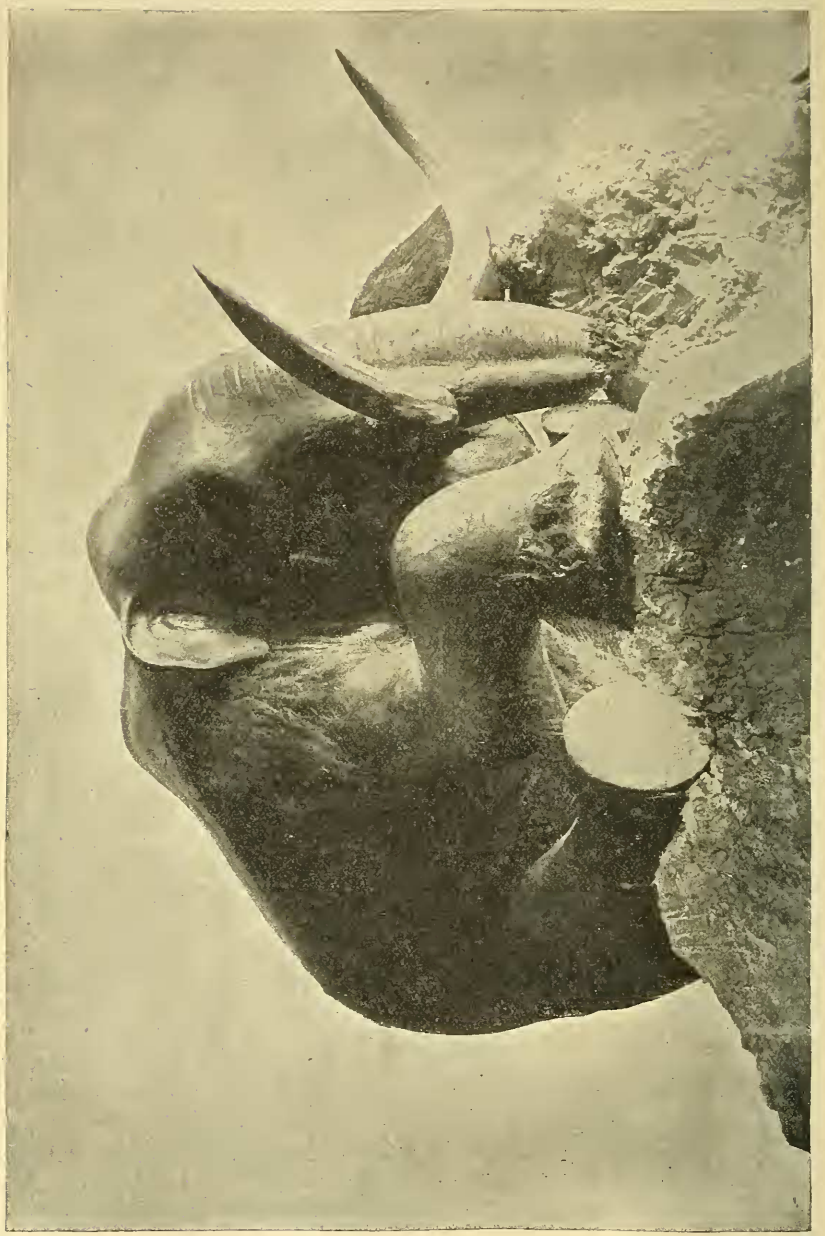

Fig. 9. Mammoth of 1901 mounted in the St. Petersburg museum; after Herz.

matter (oxide of manganese). It is especially interesting to note that the people of that day were not only sufficiently advanced to have artists of a very high order, but that they also had begun to domesticate the horse, if one may judge from the indications of harness on some of the equine figures. The horse is a most potent factor in the civilization of mankind.

In the caverns of Fond de Gaume in southern France there are at least eighty pictures, largely those of reindeer but including two of the mammoth. The actual association of man and the mammoth in America has not been proven. In Afton, Oklahoma, is a sulphur spring from which have been brought

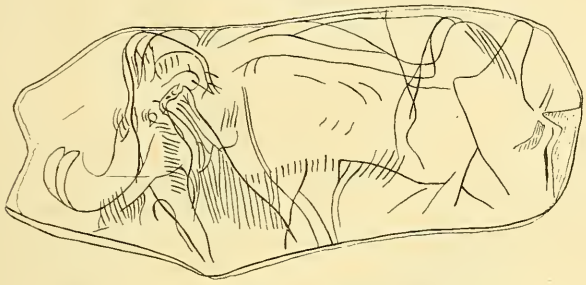

FIG. 10. Charging Mammoth; after Lubbock.

to light remains of the mammoth *(Elephas primigenius)* and mastodon *(Mammut americanum)* and numerous other animal remains, such as the bison and prehistoric horses. In the spring there were also found numerous implements of flint, mainly arrowheads. This naturally was first interpreted as an instance of actual association of mankind and the elephants, but careful investigation proved that the elephant remains far antedated the human relics, and that the latter were votive offerings cast into the spring by recent Indians as a sacrifice to the spirit occupant, the bones being venerated as those of their ancestors (Holmes). Another instance, not of the association of the mammoth with mankind, but of the mastodon, is probably authentic. This was in Attica, New York, and is reported by Professor J. M. Clarke. Four feet below the surface of the ground in a black muck he found the bones of the mastodon, and twelve inches below this, in undisturbed clay, pieces of pottery and thirty fragments of charcoal (Wright). The remains of the mastodons and mammoths are very abundant in places, the Oklahoma spring already mentioned producing 100 mastodon and 20 mammoth teeth, while the famous Big Bone Lick in Kentucky has produced the remains of an equal number of fossil mastodons and elephants.

Indian tradition points but vaguely to the proboscidians, and one cannot be sure that they are the creatures referred to, yet it would be strange if such keen observers of nature as the American aborigines should not have some tales of the mammoth and mastodon if their forefathers had seen them alive. One tradition of the Shawnee Indians seems to allude to the mastodon, especially as its teeth led the earlier observers to suppose that it was a devourer of flesh. Albert Koch, in a small pamphlet on the Missourium (mastodon) discovered by

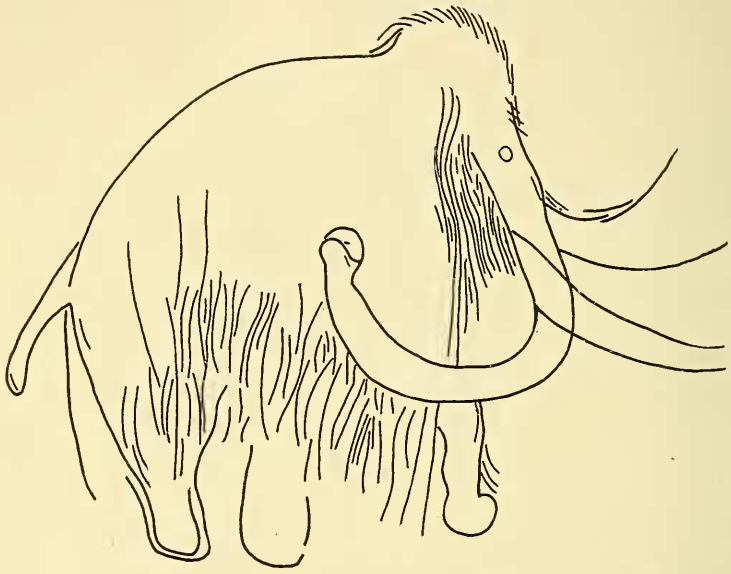

Fig. 11. Painting of Mammoth on wall at Combarelles; after MacCurdy.

him in Osage county, Missouri, and published in 1843, gives the tradition as follows:

"Ten thousand moons ago, when nothing but gloomy forests covered this land of the sleeping sun,—long before the pale man, with thunder and fire at his command, rushed on the wings of the wind to ruin this garden of nature,—a race of animals were in being, huge as the frowning precipice, cruel as the bloody panther, swift as the descending eagle, and terrible as the angel of night. The pine crushed beneath their feet and the lakes shrunk when they slaked their thirst; the forceful javelin in vain was hurled, and the barbed arrows fell harmlessly from their sides. Forests were laid waste at a meal and villages inhabited by man were destroyed in a moment.

The cry of universal distress reached even to the regions of peace in the West; when the good spirit intervened to save the unhappy; his forked lightnings gleamed all around, while the loudest thunder rocked the globe; the bolts of heaven were hurled on the cruel destroyers alone, and the mountains echoed with the bellowings of death; all were killed except one male, the fiercest of the race, and him even the artillery of the skies assailed in vain; he mounts the bluest summit that shades the sources of the Monongahela, and roaring aloud, bids defiance to every vengeance; the red lightning that scorched the lofty fir, and rived the knotty oak, glanced only on this enraged monster, till at length, maddened with fury, he leaps over the waves of the West, and there reigns an uncontrolled monarch in the wilderness, in spite of Omnipotence."

Part II.

The Early Proboscidians.

Mœritherium.

The earliest known genus of proboscidians is *Mœritherium*, a small, tapir-like form, from the Middle Eocene Qasr-el-Sagha

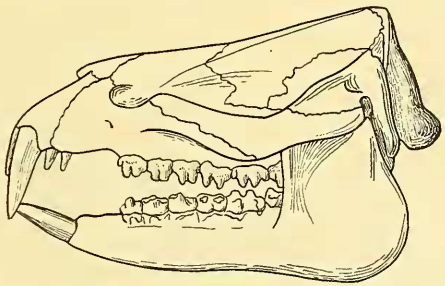

Fig. 12. Mœritherium skull; after Andrews ($\times \frac{1}{7}$).

beds of the Fayûm in Egypt. This creature was probably a dweller in swamps, living upon the succulent, semi-aquatic herbage of that time. It has little that suggests the elephants of later days and, were it not for transitional forms, would hardly be recognized as a proboscidian at all. However, one can see the beginnings of distinctively elephantine features. The hinder part of the cranium is already beginning to develop the air cells or diploë, the nostril opening and nasal bones are commencing to recede, indicating the presence of a prehensile upper lip, and the reduction of the teeth has begun, the second pair of incisors in each jaw being already developed as tusks. Those of the upper jaw were dagger-like, and

downwardly projecting, while the lower ones were directed forward, their combined upper surface forming a continuation of the spout-like union or symphysis of the jaws. The molar teeth, 24 in number, bore on the crown four low tubercles partially united into two transverse crests. The neck was of sufficient length to enable the animal readily to reach the ground, though the prehensile lip must have been used for food-gathering. Our knowledge of the creature's bodily form is imperfect, as a complete skeleton has not been found. *Mœritherium* measured about 3½ feet in height, and existed up into the Upper Eocene as a contemporary of *Palæomastodon*, doubtless owing to a continuation of those favorable conditions under which it lived.

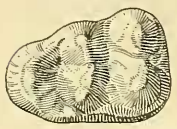

Fig. 13. Tooth of Mœritherium ($\times \frac{1}{2}$).

Palæomastodon.

Palæomastodon of the Upper Eocene was more elephant-like than its predecessor, *Mœritherium*, and of larger size, while its limbs were much like those of more modern types. The skull has increased materially in height, with a consider-

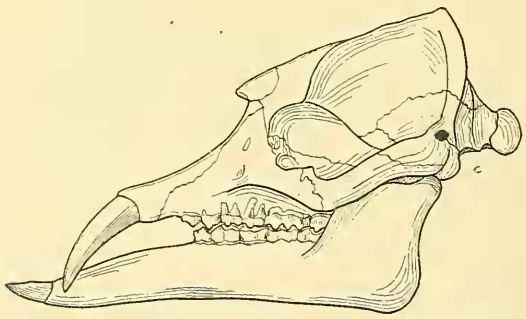

Fig. 14. Skull of Palæomastodon ($\times \frac{1}{12}$); after Andrews.

able development of air cells in the bones. The small nasals with the nasal openings had receded so that they lay just in front of the orbits, much as in the tapir of to-day. This would imply the development of a short extensile proboscis, essentially like that of the modern elephant except for size. The upper and lower canines and incisors have entirely disappeared except the second pair of incisors in each jaw, which have become well-developed tusks. Those of the upper jaw are large, downwardly curved, and with a band of enamel on the outer face. The lower jaw has elongated considerably, especially at

the symphysis, and the lower tusks point directly forward as in *Mœritherium*. The proboscis possibly did not extend beyond the lower tusks while at rest, though it could probably be extended beyond them. The premolar teeth have two while the molars have three transverse crests composed of distinct tubercles and the cingulum of the hindermost tooth shows a strong tendency to form yet another crest. There were twenty-six teeth altogether. The neck is still fairly long, though the hinder neck vertebræ are beginning to shorten.

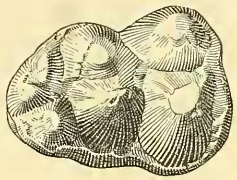

Fig. 15. Tooth of Palæomastodon ($\times \frac{1}{2}$).

Palæomastodon is confined to the Upper Eocene, and has thus far been found only in the Fayûm region.

The Yale collection includes full-sized restorations of the skulls of *Mœritherium* and *Palæomastodon* as well as casts of the type specimens, gifts of the British Museum of Natural History.

Classification of the Later Proboscidea.

We know as yet no Oligocene proboscidians, the next forms being found in the lower Miocene of northern Africa and Europe, so that a considerable break occurs in the continuity of our series. It is evident that the line was still African in distribution, for apparently the exodus from Egypt did not occur before Miocene times.

The mastodons have been divided in two ways, one depending upon the number of ridges borne upon the grinders, while the other classification is based upon the number and character of the tusks. The latter seems the more logical from a developmental viewpoint. The first of these genera is *Tetrabelodon*, with four, enamel-banded tusks. The second is *Dibelodon*, having but two tusks which still retain the band of enamel. The last genus is *Mammut*, with enameless upper tusks in the adult, though one or two may also be present in the adolescent lower jaw. The latter are sometimes retained throughout life.

Tetrabelodon.

The third recorded stage in the evolution of the elephants is represented by the Miocene *Tetrabelodon angustidens*, of which a splendid specimen from Gers, France, is preserved in the museum of the Jardin des Plantes at Paris. It was an animal of considerable size, nearly as large as the Indian elephant, but differing markedly from the latter in the peculiar character of the lower jaw, which was enormously long at the symphysis and contained a pair of relatively short tusks. This form represents the culmination of the jaw elongation, for in its successors the symphysis is rapidly shortened and the infe-

rior tusks finally disappear. The upper tusks in *Tetrabelodon* were longer than those of the lower jaw but did not extend much beyond the latter. The tusks had an enamel band upon the outer and lower face and were slightly curved downward. The nasal orifice had receded farther to the rear, indicating a still greater development of the trunk than in *Palæomastodon*.

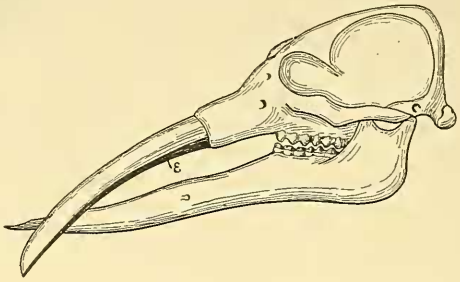

Fig. 16. Skull of *Tetrabelodon angustidens*.

The proboscis, still supported from beneath by the rigid lower jaws, could only be raised and moved from side to side. The neck is now quite short, so much so that were it not for the proboscis and tusks this creature could not reach the ground. Both upper and lower tusks show signs of wear which could only be caused by digging, those on one side being often much more worn than on the other.

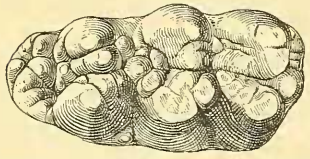

Fig. 17. Tooth of *Tetrabelodon angustidens* ($\times \frac{1}{4}$).

The teeth have increased in size to such an extent that but two adult grinders at a time can be contained in each half of the jaws.

Tetrabelodon was a widely spread, migratory form, for we find species referable to this genus not only in Europe but in Africa, Asia, and in North America. In Eurasia it gave rise to *Mammut* through the loss of the lower tusks and the enamel band, while in America there arose *Dibelodon*, which retained the enamel band and which was the first proboscidian to reach South America after the formation of the Central American land connection either late in the Miocene or in the early Pliocene.

The Yale Museum contains fine specimens of teeth and tusks of *Tetrabelodon angustidens* from France as well as similar remains of *Tetrabelodon poavus*, *T. campestæ*, *T. productus*, and *T. serridens*. In the Yale Museum is also pre-

served part of the holotype of *Tetrabelodon shepardi* Leidy from California, of which the remainder is in the museum of Amherst College.

Dibelodon.

The genus *Dibelodon* is known principally from the jaws, teeth and tusks, though two splended skulls of *D. andium* are preserved in the Museo Nacional in Buenos Aires. The upper

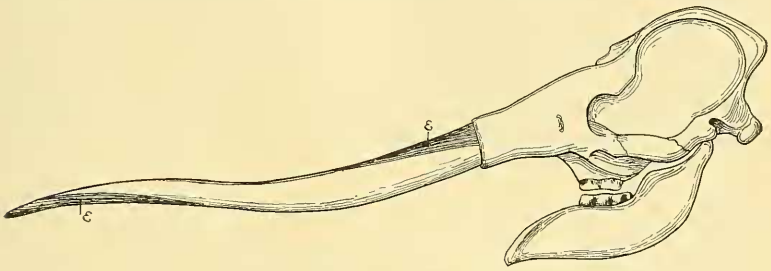

FIG. 18. Skull of *Dibelodon andium*.

tusks are well developed, displaying an elongated spiral form, with a well developed enamel band, but the lower jaw is quite short though the symphysis is longer and more trough-like than in the genera *Mammut* and *Elephas*. The lower tusks have entirely disappeared and with the shortening of the jaw the trunk must have become pendant as in the modern elephants.

The genus *Dibelodon* contains several species, among which are *Dibelodon humboldii* (Cuvier), *D. mirificium* (Leidy), *D. præcursor* (Cope), and *D. andium* (Cuvier). Of these *Dibelodon humboldii* and *D. andium* ranged into South America and were in fact almost the only proboscidians to cross into the southern hemisphere of the New World. Some of these animals lived in the high Andes at an elevation of 12,350 feet above the level of the sea, at a time when the region had a greater rainfall than now and therefore a richer vegetation.

The Yale collection contains teeth and portions of the tusks of *Dibelodon mirificus* and *D. obscurum* as well as of *D. humboldii*. One *D. obscurum* specimen is part of that figured by Leidy, the remainder being in the Amherst College Museum. There are also preserved at Yale a femur and an axis probably referable to *Dibelodon andium*, from the Pliocene Bone Bed of Quito valley, South America, found at an altitude of 10,000 feet.

Mammut.

This genus reaches its culmination in the American mastodon, a creature of great bulk, though about the height of the Indian elephant. It was, however, much more robust, a feature especially noticeable in the immense breadth of the pelvis and the massiveness of the limb bones. The feet were more spreading than in the true elephants, which, together with the character of the teeth, and the conditions under which the remains are found, points to different habits of life from those of the mammoth, the mastodons being more distinctively forest-dwelling types. The skull differs from that of the true elephants in its lower, more primitive contour, for while there is a large development of air cells in the cranial walls the brain cavity is relatively larger. The tusks are well-

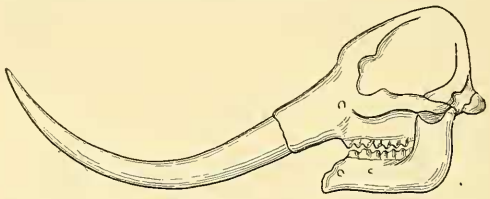

Fig. 19. Skull of the American Mastodon.

developed, powerful weapons, not so sharply curved as in the elephants, though in this respect individuals vary. The tusks are very heavy at the base and taper rapidly, curving inward at the tips. In the lower jaw the tusks are vestigial, being apparently present only in the male. Usually they are soon shed and the sockets may entirely disappear as in the Otis-

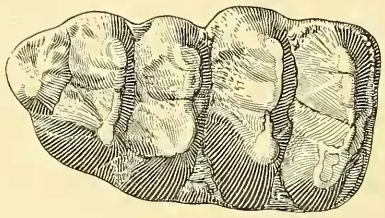

Fig. 20. Tooth of Mastodon ($\times \frac{1}{4}$).

ville mastodon at Yale, whereas the Warren mastodon now in the American Museum, a fully adult animal, retained the left lower tusk, which is about eleven inches in length. The socket of the right tusk is also still distinct. A cast of the symphysis of the lower jaw of a young animal containing one tusk is exhibited at Yale.

The grinding teeth were of large size, two in each half of either jaw, as in the *Tetrabelodon*, but the crests are simpler with but few accessory cusps. The crown of the tooth is covered with thick enamel, which in turn is overlain by a thin layer of cement before it cuts the gum. This is soon removed by wear. These teeth are admirably adapted for crushing succulent herbage such as leaves and tender twigs and shoots, but not for grinding the siliceous grasses which form a necessary part of the food of the true elephants. "Broken pieces of branches varying from slender twigs to boughs half an inch long" have been found within the ribs of a mastodon together with "more finely divided vegetable matter, like comminuted twigs to the amount of four to six bushels." "Twigs of the existing conifer *Thuia occidentalis* were identified in the stomach of the New Jersey mastodon, while that of Newburgh, N. Y., contained the boughs of some conifer, spruce or fir, also other not coniferous, decomposed wood. A newspaper account of the finding of the great Otisville mastodon, now preserved at Yale, says that the region of the stomach contained "fresh-looking, very large leaves, of odd form, and blades of strange grass of extreme length and one inch to three inches in width."

The Yale collection contains numerous specimens of the American mastodon, including the nearly complete skeleton from Otisville, N. Y., soon to be mounted, another fairly complete skeleton of a younger individual from Urbana, Ohio, and many jaws and teeth. There are also specimens of the apparently ancestral *M. borsoni* from England.

True Elephants.

In order to trace the evolution of the true elephants we must go back once more to the Upper Miocene of southern India to the form known as *Mammut latidens*. This creature gave rise to a species variously known as *Mastodon elephantoides* or *Stegodon clifti*, for its transitional character is such that authorities differ as to whether it is a mastodon or an elephant.

Stegodon.

In *Stegodon* the molar teeth have more numerous ridges than in the true mastodons and the name *Stegodon* is given because of the roof-like character of these ridges, the summits of which are subdivided into five or six small, rounded prominences. There is a thin layer of cement over the enamel in an unworn tooth but no great accumulation in the intervening valleys as in the elephants. These teeth show how slight the transition is, however, merely a filling of

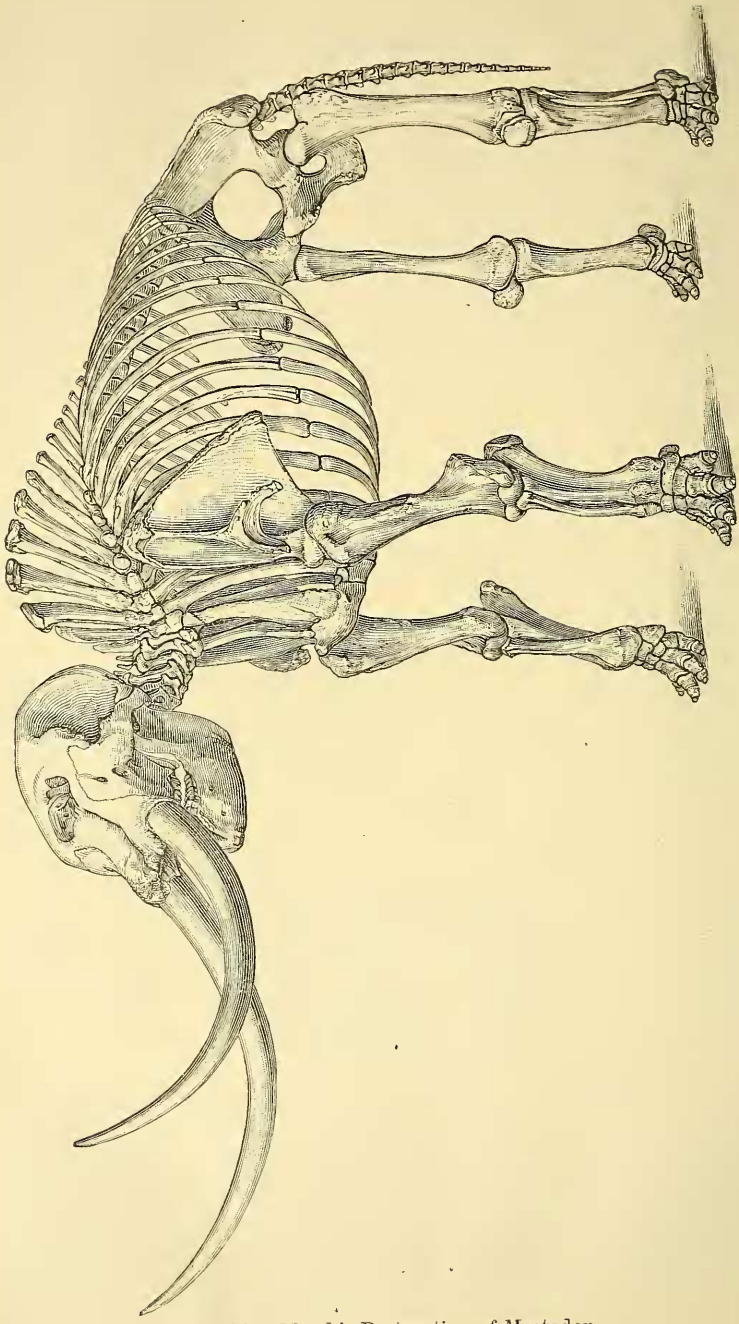

FIG. 21. Marsh's Restoration of Mastodon.

cement to bind the crests together and the elephant tooth is formed.

Stegodon embraces at least three species, the home of which was central and southern India, though two of them ranged east as far as Japan, then united to the Asiatic continent. *Stegodon insignis* lived into Pliocene times. Of the transitional forms, the Yale Museum contains casts of the type specimens of *Mammut latidens* and *Stegodon clifti*. True elephants, derived from the Stegodonts, existed in India, their remains being found in the Siwalik hills.

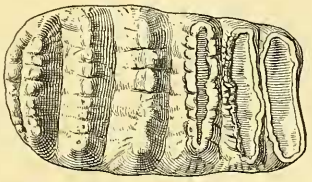

Fig. 22. Stegodon tooth ($\times \frac{1}{4}$).

During Pliocene times there existed in Europe two immense elephants known as *Elephas meridionalis* and *E. antiquus*, each of which lingered on into the cooling climate of the Pleistocene. The former, while ranging as far north as England, was more southerly in general distribution and of a size which has probably never been exceeded except possibly by *Elephas imperator* of North America. A mounted specimen of *Elephas meridionalis* in the Natural History Museum of the Jardin des Plantes at Paris, France, measures thirteen feet and one inch at the shoulder and probably exceeded this in the flesh. The tusks are massive but do not reach the extreme of development of the later mammoths, while the teeth have rather coarse lamellæ.

Elephas antiquus stands midway in character between the African and Indian elephants of to-day. The tusks were nearly straight and the creature was also of great size. It is first found in the Lower Pleistocene (Forest Beds) of Norfolk, England. In the Thames valley deposits it was contemporaneous with early man and, for a while, with *Elephas primigenius*, the hairy mammoth. *E. antiquus* was essentially an animal of warm climate, giving way to the mammoth when the arctic conditions of the glacial period arose.

Elephas antiquus is represented at Yale by a fine cast of the skull, jaws, a tusk and other bones from the Belgium Royal Museum, while of the early elephants of India there are three casts of skulls recently presented by the British Museum of Natural History.

In North America, during the cooling to cold climatic condi-

tions of Pleistocene time, there were three species of *Elephas* of which the most primitive in point of tooth structure was the great imperial elephant, *E. imperator*, a migrant from the Eurasian continent. This species appeared in the Lower Pleistocene (Equus or Sheridan beds) and, while it ranged from Ohio to California, was more southern in distribution, ranging as far as Mexico and possibly into French Guiana. In this species the grinding teeth were of enormous size with very coarse lamellæ and the outer covering of cement was extremely thick.

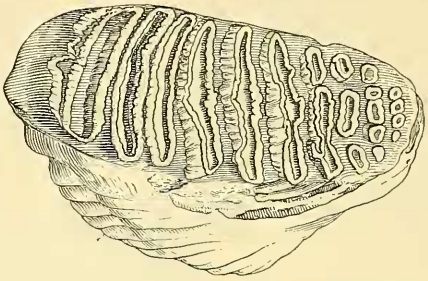

Fig. 23. Tooth of *E. imperator* (× ¼).

Elephas imperator was of great size, 13½ feet in height at the shoulder, and the huge, spiral tusks measured thirteen feet along the curve by 22 inches in circumference. One tusk in the city of Mexico is said to be sixteen feet in length! The collection at Yale contains one molar tooth of *Elephas imperator* from Mexico, one from Ohio, and the right ramus of the lower jaw containing a single molar from Alameda county, California. An upper molar of this same individual is in the

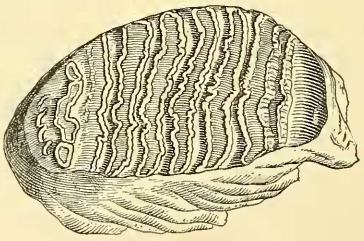

Fig. 24. Tooth of *E. columbi* (× ¼).

Amherst College museum, while a portion of the tusk is in that of Wabash College.

Elephas columbi, the Columbian mammoth, is thought by some authorities to be but a variety of *E. primigenius*, the teeth being transitional in the character of the lamellæ between

the latter and *E. imperator*. In fact, they greatly resemble those of the modern Indian elephant. *E. columbi* was early and middle Pleistocene in distribution, more southern in range than *E. primigenius*, though the two inhabited a broad frontier belt along the northern United States. *E. columbi* reaches the maximum of evolution in the shortening and heightening of the skull. The tusks in a mounted specimen in the American Museum of Natural History are so huge that their tips actually curve backward and cross each other. They have completely lost their original digging function and their use as weapons must have been much impaired. They seem to represent an instance of a certain acquired momentum of evolution carrying them past the stage of greatest usefulness to become an actual detriment to their owner. This may have been an important factor for extinction. Specimens at Yale referable to *E. columbi* consist of several molars from Idaho, Florida, California, and Mexico.

Elephas primigenius.

The mammoth was not among the largest of elephants, being but little in excess of *Elephas indicus* in height, but with

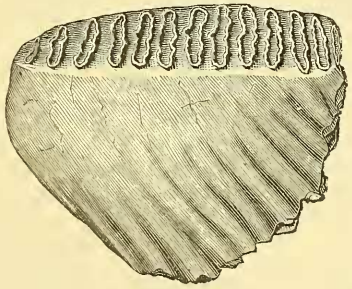

Fig. 25. Tooth of *E. primigenius* ($\times \frac{1}{4}$); after Marsh.

relatively huge tusks exceeding, in some instances, a length of over eleven feet measured along the outer curve. The teeth have the most numerous and finest lamellæ, and in this respect, as well as in the development of hair, this creature shows the greatest degree of specialization as compared with the tusks and skull in the Columbian species. It is curious to note, however, that in three ways one can trace the increasing fineness in the lamellæ of the molars corresponding to the three modes of distribution,—latitude, altitude, and time,—for the more ancient individuals, living the farthest south and nearest the sea-level, have teeth very much like those of *E. columbi*. The increasing fineness of lamellæ is correlated with increasing cold and a consequent change in the character of food plants, as the last of the

mammoths fed upon harsh grasses and the needles and cones of the fir and other conifers, mingled with moss. The hairy coat, another adaptation to extreme cold, was of three sorts, an inner coat of reddish wool, next a longer, fawn-colored coat outside of which were long, black bristles, especially on certain parts of the body, as the neck, back, and chest. It is interesting to note that in the Indian elephant, the nearest living ally of the mammoth, there is, at birth, a complete coat of rather long hair which is shed in a few weeks except that in the mountain region of the Malay peninsula elephants are reported to be persistently hairy. This points to an ancestral hairy condition atavistically developed in later types when necessitated by cold. A similar development is seen in the Manchurian tiger, in form and markings precisely like its tropical cousin, the sleek Bengal tiger, but with a long, thick fur which defies the cold of a climate as severe as that of New England.

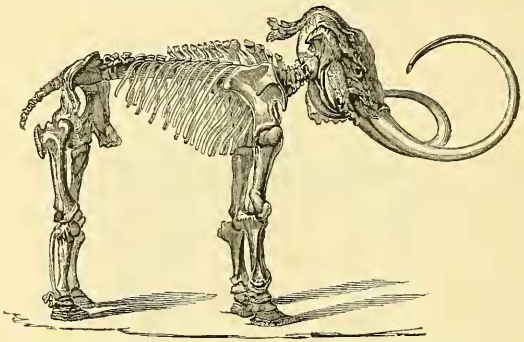

Fig. 26. St. Petersburg Mammoth of 1806.

The hairy mammoth was circumpolar in distribution, ranging from Europe across the north of Asia as far as 70° north latitude to the eastern part of the United States, its southern limit overlapping the northern range of *Elephas columbi*.

Of *Elephas primigenius* the museum at Yale contains several important specimens: Molar teeth from Minnesota and Washington state. A fine jaw from Nebraska with teeth nearly as coarsely ridged as those of *Elephas columbi*. Molars from England and Siberia, tusks from Alaska, hair from an Alaskan ice cliff and a piece of hide from the Siberian mammoth brought to St. Petersburg, Russia, in 1806.

Modern Elephants.

The African elephants are the more primitive in the character of the teeth with their broad lozenge-shaped lamellæ, unless, as has recently been suggested, they are in this respect degenerate. The African forms included by some authorities under

the genus *Loxodonta* have recently been divided into four species. They are distinguished from their cousins of India by the contour of the head, the greater size of the ears, greater development of the tusks, and the presence of two figure-like processes at the tip of the proboscis instead of but one. African elephants reach a greater size than do those of India, attaining a height of twelve to thirteen feet at the shoulders and a weight of over seven tons.

The Indian elephant includes but one species, *E. indicus*, of which there are, however, several well-marked castes or breeds, varying greatly in commercial value. In size the Indian elephant rarely reaches eleven feet, averaging about nine for the males. The high, convex forehead gives the Indian elephant a somewhat nobler, more intellectual cast of countenance than its African cousin, but this character is due solely to the greater development of the air cells in the skull.

Dinotherium.

In the Miocene of Europe, though ranging up into the Pliocene of Asia, is a curious aberrant type, evidently a probosci-

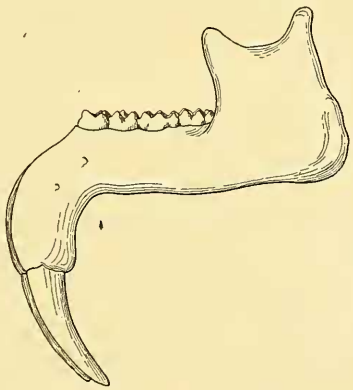

Fig. 27. Jaw of Dinotherium; after Kaup.

dian though formerly classed with the Sirenia. This form is *Dinotherium* and must have been derived from some very early genus, certainly not later than *Palæomastodon*. The teeth differ from those of the elephants in their greater number and in their mode of succession, being more like those of other mammals. The grinding teeth are extremely simple, the premolars having three while the molars have but two cross crests with open, uncemented valleys. Tusks are apparently confined to the lower jaw, no trace of upper tusks having been

seen in the only known skull, now unfortunately lost. Those of the lower jaw were large and, together with the elongated symphysis, bent abruptly downward, the tips being actually recurved. The skeleton, so far as known, indicates a huge elephant-like body and limbs and the impression is that the creature must have been semi-aquatic, frequenting the beds of streams and living upon the succulent herbage which it rooted up by means of its tusks. The contour of the skull is ill known, so that, with the exception of the lower jaw, restorations of the head are largely conjectural. Dinotherium died out in the Pliocene, leaving no descendants.

Part III.

Migrations of the Proboscidea.

In studying the dispersal of a group of terrestrial vertebrates one has to consider not alone the probability of land bridges over which the wandering hordes might pass, but, on the other hand, the existence of barriers to migration other than the absence of these bridges.

The possible barriers are climatic, topographic, and vegetative. Of these the climatic has been given weight, but in the case of the proboscidians the direct action of temperature is relatively unimportant, though the presence of moisture is a prime necessity.

The African elephant formerly ranged from Cape of Good Hope into Spain, while *Elephas primigenius* enjoyed an even greater range in latitude and consequent temperature. The African species has a vertical distribution from sea level to a height of 13,000 feet in the Kilimanjaro region, which also gives a great range of climatic variation. Aridity, however, is a most efficient barrier, not only from its effect upon the food supply, but because water is a prime necessity to elephantine comfort. The Sahara to-day marks the northernmost limit of the African species, the former distribution to the north being by way of the Nile valley or possibly to the westward of the great desert.

Mountain ranges on the whole do not impede elephant migration, except of course such mighty uplifts as the Himalayas. The height to which the elephant wanders in the Kilimanjaro has already been mentioned, while Hannibal took a number of African elephants across the Little St. Bernard pass, which has an altitude of 7,176 feet, in his invasion of Italy in 218 B. C. The Pyrenees, however, seem to have prevented the numerous elephants of France from invading the adjacent Spanish peninsula, as the few species of fossil

elephants found therein seem almost without exception to have entered from Africa by way of Gibraltar. The great ranges of mountains in the new world may have influenced somewhat the trend of migration, but were crossed by the proboscidians at will.

Vegetation does constitute a most effective barrier, especially in the case of the tropical jungle of central America. During the Pliocene, as we shall see, after the land bridge was established, intercommunication between the two Americas was very free. In the Pleistocene, however, this migration of large quadrupeds gradually ceased, so that in spite of the great abundance of mammoths and mastodons in North America none attained a foothold south of the Mexican plateau. To-day the jungle is absolutely impenetrable for all of the larger mammals except such as may be at least partially arboreal in habits.

The migrations were forced, not voluntary, for it would appear that the mighty elevations of Asia beginning in late Miocene times and the consequent alternations of moist and arid climates, with a strong tendency toward the latter, has caused these great animals to disperse themselves from the rising high lands of central Asia into the more stable low lands. In these forced wanderings the land bridge between Asia and Alaska was again and again discovered and crossed by the migrating hordes.

The first appearance of the proboscidians is in the Middle Eocene beds of the Egyptian Fayûm district. There we find in *Mœritherium*, the most primitive type, the forerunner of the race. Of the extent of the geographical range of *Mœritherium* and of its successor, *Palæomastodon*, we know nothing further than that they have only been found within the Fayûm.

During the Oligocene the proboscidians seemingly remained in Africa, though of this we have no record. Early Miocene deposits of Mogara, which lies northwest of the Fayûm some five days' journey, about 75 miles, give us the remains of *Tetrabelodon angustidens*, the next known type in the evolutionary series. From Tunis again this species is reported, being what Professor Deperét calls the ancestral (ascending mutation) race of *T. angustidens, pigmæus*. This race is also reported from the sands of Orleans and from the Burdigalienne of Agles (Aglie, Italy). Thus it seems as though *Tetrabelodon angustidens*, the form with the maximum development of symphysis, were the one to make the exodus from Africa, not as the children of Israel did, by way of the northeast, but by the land bridge connecting Tunis with Sicily and the latter with Italy, and thence, by way of Greece to Europe and Asia.

Mammut americanum phylum.

(See Chart 1.)

Tetrabelodon angustidens did not go unaccompanied, for another type, *Tetrabelodon turicensis* (=*tapiroides*), found in the Lower Miocene of Algeria, must have travelled into Europe by the same route and about the same time. In *T. turicensis* the grinders are simple in character as though it had already begun to differ in its feeding habits from its contemporary, in which the teeth are comparatively complex. *Tetrabelodon turicensis* spread during the Miocene over France, Germany, Austria-Hungary, Russia and as far as southeastern Siberia. The successor of *Tetrabelodon turicensis* was *Mammut borsoni*, covering much the same geographical area as its forebear, being found as far as England to the north and Russia, along the northern coast of the Black sea, to the east. Geologically it ranges from Lower to Upper Pliocene. *M. borsoni* merges into *Mammut americanum*, the great American mastodon which outlived the mammoth in the New World. Some teeth found in southeastern Russia have been referred to the American type by Mme. Pavlow, who was perfectly familiar with *M. borsoni*. However that may be, the migration of this race was without doubt across Siberia, the Behring isthmus and into the New World from the northwest. The American mastodon's remains have been found from Alaska to California, east to Prince Edward's Island and from Hudson Bay to Florida on the east coast, while Le Conte reports a specimen from Tambla, Honduras, about 15° north latitude, the nearest recorded approach to South America.

Tetrabelodon—Dibelodon phylum.

Tetrabelodon—Elephas phylum.

(See Chart 2.)

Reverting once more to *Tetrabelodon angustidens*, we find in it the possible ancestor of all of the later proboscidians, with the exception of the very aberrant *Dinotheres* and the American mastodon phylum. *Tetrabelodon angustidens* was a great migrant covering most of Europe with the exception of Spain and England. Its descendants diverged along several lines of specialization as along varied lines of travel, at least one representative reaching North America in the Middle Miocene (Deep River beds), possibly before (Virgin Valley of Oregon (Merriam)). The earliest North American form, *Tetrabelodon productus*, resembled its European prototype very closely and

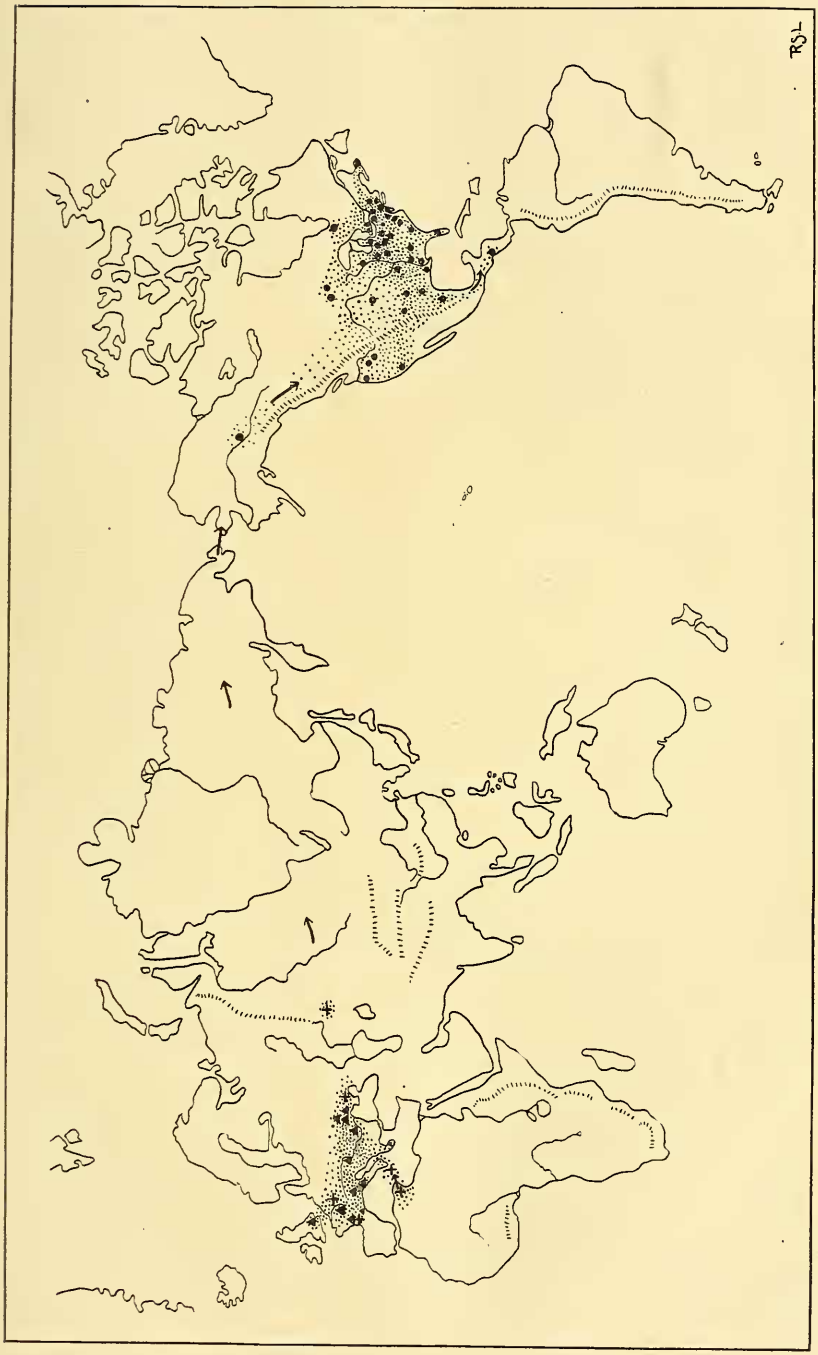

CHART 1. Miocene-Pleistocene. Mammut americanum Phylum.
+ Tetrabelodon turicensis. ● Mammut americanum.
▲ Mammut borsoni.

gave rise to a remarkable group of four-tusked mastodons which ranged from Nebraska to Florida. From some of the later species arose the *Dibelodon* race with upper, enamel banded tusks, but lacking those of the lower jaw. This genus is reported from the Pliocene (Blanco) of Texas and Mexico and ranges as far south as Buenos Aires in the southern hemisphere. Two South American species are known to us, one, *D. andium*, following the chain of the Andes as far south as Chili. This type is often found at great altitudes, a specimen from the Quito valley in Ecuador, now in the Yale collection, having been found 10,000 feet above the level of the sea.

Dibelodon humboldii was a dweller on the plains, being found in the pampas formation near Buenos Aires, while Darwin records it along the banks of the Parana river in Argentine, and Wallace reports the same species among other remains in a limestone cavern near the headwaters of the San Francisco river in southern Brazil. *D. humboldii*, like *D. andium*, has its origin in the Texas Pliocene, the line of migrations nearly paralleling, the one along the tropical plains, the other along the Andine plateau as far south as northern Chili. With the exception of a lone specimen of *Elephas* reported from French Guiana and the mastodon of Honduras, *Dibelodon* is the only proboscidian of the Neotropical realm. The migration of these great forms occurred in the late Pliocene, and for some reason, evidently climatic and vegetative, the route has been closed ever since. Otherwise it is reasonable to suppose that the elephants and mastodons of the Pleistocene would have spread into South America as well.

In Europe *Tetrabelodon angustidens* had successors in *T. longirostris* and *arvernensis*, the latter ranging over western Europe into England. It did not, however, cross the Pyrenees into Spain. *T. longirostris* and a late mutation of *T. angustidens*, *palæindicus*, made the long journey to the Orient, transferring the evolution from Europe to India. The path of this migration is as yet unknown, as little or no paleontological exploration has been made in the region lying between Armenia on the west across Persia, Afghanistan, and Beluchistan to the Indus river. This oriental migration must have occurred during the Upper Miocene and was followed by a relatively rapid evolution involving a number of species of mastodons and elephants. *Tetrabelodon longirostris* seems to have given rise to *Mammut** *cautleyi* with a shortened lower jaw, thence through *M. latidens* to *Stegodon clifti*, the transitional form between the mastodons and the elephants. *S. clifti* was followed

* These Indian forms agree probably with the American mastodon in having but one pair of enamelless tusks. They may represent the *Mammut* stage but in an entirely different phylum, hence should not bear the same generic name.

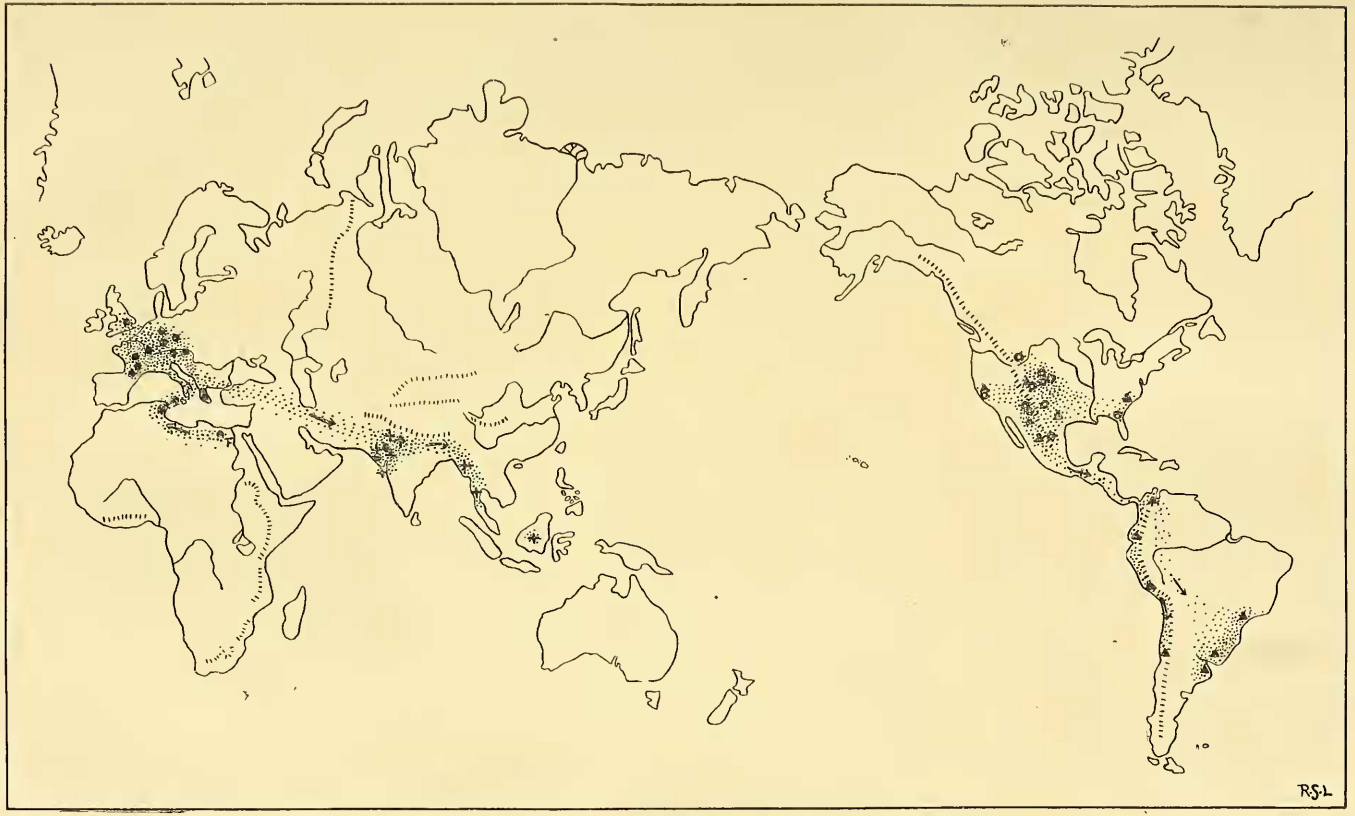

CHART 2. Miocene–Pliocene. Tetrabelodon-Elephas Phylum (part). Tetrabelodon-Dibelodon Phylum.

F Fayûm.
● Old World Tetrabelodon.
+ Old World Mammut (leading to Stegodon).
○ New World Tetrabelodon.
▲ New World Dibelodon.

in succession by *Stegodon bombifrons* and *S. insignis* and finally by the genus *Elephas* itself. *Elephas* proved to be a great migrant, although the stegodont species had spread from their original homes in the sub-Himalayan region eastward through Burma, China, and Japan and perhaps as far as Java. *Elephas* later travelled in two directions, westward back to Europe and Africa, and eastward, thousands of miles, into the United States.

Evidence seems to point to an interesting parallelism in evolution between the American elephants and those of Europe, though they were undoubtedly derived from a common ancestry.

The True Elephants.

(See Chart 3.)

Disregarding for the present the hairy mammoth, *E. primigenius*, two notable types are found in Europe during Pliocene and Pleistocene times. Of these the more ancient is *Elephas meridionalis*, probably derived from *Stegodon insignis* of India and undoubtedly the migratory species over the Persia–Asia Minor route which the remote ancestors travelled in their journey to the East.

Elephas meridionalis ranges from the Red Crag (Upper Pliocene) to the Lower Pleistocene Forest Beds and from England on the north to Algeria on the south, though never gaining a permanent foothold in Africa. *E. meridionalis* is succeeded by *E. antiquus*, a great form with straight tusks, whose geological range is from the Forest Beds to the Upper Pleistocene. *E. antiquus* is found in England, central Europe, as far east as the region lying north of the Black sea. In a southerly direction one can trace the course of migration through Italy, Malta, Sicily, north Africa, and across the present strait of Gibraltar to southern Spain, where specimens have been found at Europa Point and at Seville. Evidently the Pyrenees proved too great a barrier for a direct migration into Spain, though the invasion was accomplished through this circuitous route. In the islands of Sicily and Malta are found relics of this southern march of *E. antiquus*, not only remains of the normal species, but of its curiously dwarfed descendants, *Elephas mnaidriensis*, *E. melitensis* and *E. falconeri*, the last only three feet high. These types developed through degeneracy after the migration had passed and the line of communication was cut off, leaving Sicily and Malta as small islands. The limited area, scanty food and general hard conditions were responsible for the dwarfing, precisely as the Shetland ponies have lost the original stature of *Equus caballus*. In the Mal-

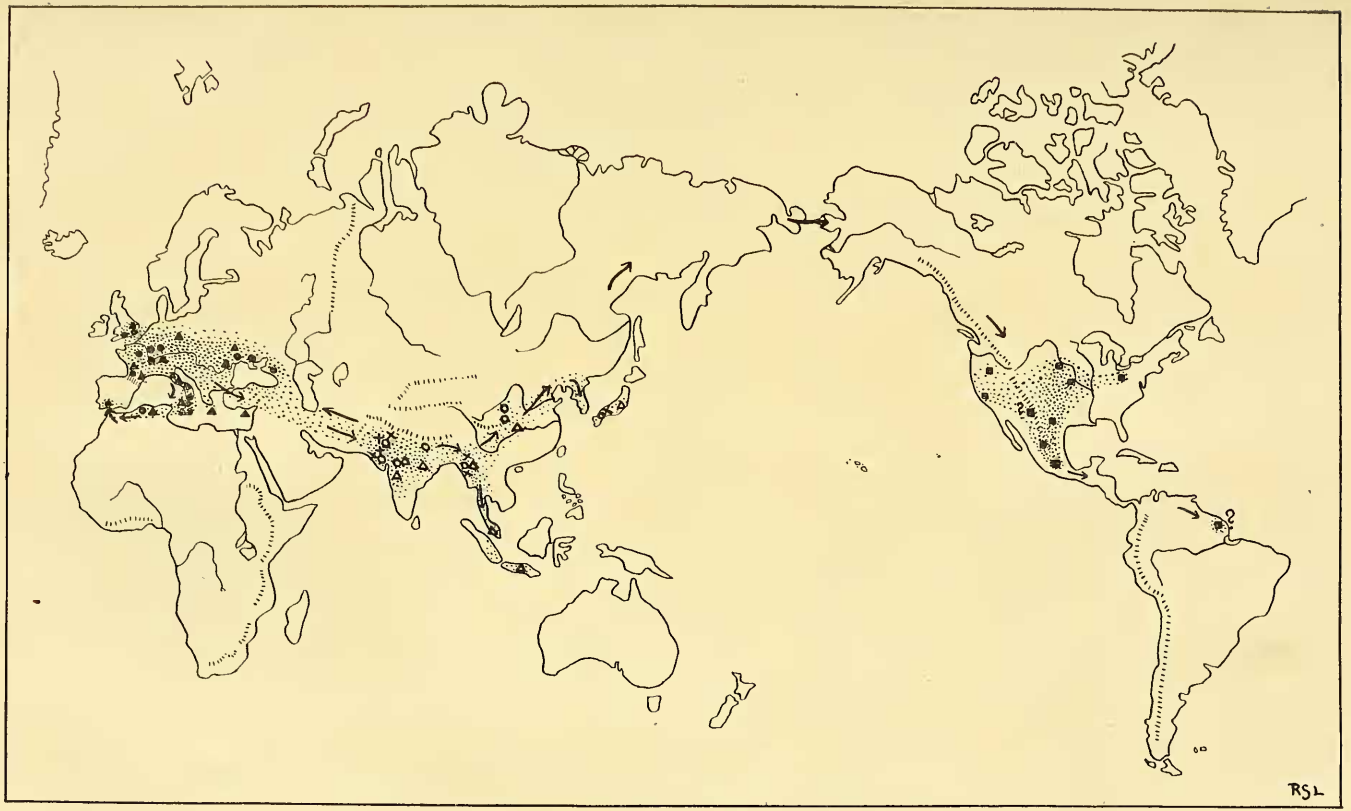

CHART 3. Pliocene-Pleistocene. Stegodon—Elephas Phylum.

× Stegodon clifti. + Elephas planifrons. △ Elephas nomadicus.
○ Stegodon insignis. ● Elephas meridionalis. □ Elephas imperator.
▲ Elephas antiquus.

tese elephants the diminution in size brings the animal *below* the stature of the ancestral *Mœritherium*, though in no other way is it an atavistic type. Dwarf forms are also found in Crete and Cyprus.

An early form of *Elephas antiquus* evidently gave rise to the modern African elephant through the type known as *Elephas priscus*, included by some authorities in *E. antiquus* itself. The development of teeth of *E. africanus* with relatively few lozenge-shaped ridges seems to be a matter of degeneracy which casts some doubt upon the value of the subgenus *Loxodonta*. *Elephas africanus* deployed over the whole of Africa with the exception of the Sahara desert. It also crossed to Gibraltar and spread over most of the Spanish peninsula. It has since been extirpated, however, in all of the region north of the Sahara. The living Indian elephant exhibits similarity of structure with the *E. antiquus*, a form known as *Elephas armeniacus*, found in Asia Minor, being annectent type. *Elephas indicus* may have come from *Elephas insignis* through the Lower Pleistocene *E. hysudricus*, and probably represents a purely local evolution, not a migratory form.

A most perplexing question arises with reference to the origin of the great North American elephants, *Elephas imperator*, *E. columbi* and finally *E. primigenius* itself. Emphasis has been placed on the similarity existing between the American and European elephants, though I know of no expression of opinion as to the actual relationship of the forms in question. In tooth characters *Elephas columbi* is certainly suggestive of its European contemporary *E. antiquus*, while *E. imperator* somewhat resembles *E. meridionalis*. The tusks which are so important from the developmental standpoint have apparently been ignored, for the American types have huge spiral tusks, while those of *Elephas antiquus* are nearly straight, and in *E. meridionalis* they show by no means the development of *E. imperator*. It is the writer's opinion that the American forms may prove to be a distinct evolution, having been derived from some such form as *Elephas planifrons*, found in India from the Pliocene of the Siwalik hills to the Pleistocene of Narbada valley. We have no record of the migration of *E. planifrons*, but its progenitors and contemporaries ranged, in some cases, as far as China and Japan by way of Burma. This being an accustomed route, *E. planifrons* or a successor might well have ventured beyond China to the northeast through Siberia, across the Behring isthmus and thence southward as far as Mexico, giving rise to the American form *Elephas imperator*, which is first reported from the Equus or Sheridan beds (Lower Pleistocene). The known range of the

Chart 4. Pleistocene–Recent. Elephas columbi-primigenius Group.

● Elephas primigenius.
Dotted area, distribution of Mammoth.
+ Elephas columbi.
//// Elephas indicus, present distribution.
\\\\ Elephas africanus, present distribution.

latter is from Nebraska to southern Mexico along the 100° meridian, although specimens in the Yale collection were found as far east as Ohio and west to the California coast. We have the authority of Lartet for the finding of a tooth of *Elephas* in the Lower Pleistocene in Cayenne, French Guiana. From the description of the "thick ridge plates" this specimen is evidently that of *E. imperator*, probably a stray to the southward before the conditions which later prohibited proboscidian migration into South America arose. It is the only recorded instance of a true elephant known to me south of the Mexican plateau. The geographical range of *E. columbi* embraced the whole southern part of the United States and the highlands of Mexico, including the area covered by *E. imperator*, with the exception of the South American locality.

Elephas primigenius phylum.

(See Chart 4.)

Elephas primigenius has been generally conceded to be of Asiatic origin and a near relative of *E. indicus*. The character of the teeth and the presence of hair in the young *E. indicus* are certainly suggestive of relationship. The teeth are also similar to those of *E. columbi* and may represent a further development of the latter type as readily as of *E. indicus* or *E. antiquus*. The presence of hair is an atavistic character developed in *E. primigenius* to meet climatic conditions, and we are by no means sure that *E. columbi* was naked, as this is simply argued from its geographical distribution. The tusks of *E. primigenius*, however, are generally the immense spirally coiled structures of *E. columbi* and *E. imperator*, though short-tusked specimens do occur, presumably young individuals. In *E. indicus* the tusks are greatly reduced, being absent in the female, often in the male, and are evidently degenerate.

Elephas columbi molars grade into those of *E. primigenius*, and there is preserved in the Yale museum a fine jaw, the characters of which are clearly those of *E. primigenius*, while the teeth are those of *E. columbi*. In fact, *E. columbi* is often regarded merely as a southern variety of the Siberian mammoth. It seems, however, as though the reverse of this statement might be true, looking upon *E. primigenius*, which is the more specialized form, as the latest mutation of the *imperator-columbi* phylum, originating in North America and becoming circumpolar in its distribution, invading Siberia from the American northwest. One tooth has been found on Long Island in the eastern part of Hudson bay, transitional in character between the mammoth and *Elephas columbi*. Lucas

supposes that this tooth may have been carried thither with a carcass or a portion of a carcass by the water or ice. This may be true, but upon such slender evidence as this we have sometimes based a route of migration which subsequent discoveries have proven true. It may in this instance imply that the migration was not wholly by way of the Behring route and that the hairy mammoth was indeed a circumpolar form.

Thus it will be seen that these majestic creatures were great wanderers, ranging in the course of time over nearly the entire world. Few mammals have been such world-wide travellers as the elephants, as their record has been exceeded only by mankind, the horses, dogs and cats, the rhinoceroses and camels pressing close behind. It would seem that in each instance the perfection of the race was in a large measure due to the development of the migratory instinct.

EXPLANATION OF FIGURES.

FIG. 1. The manatee, *Manatus australis;* after Brehm.

FIG. 2. Conies, *Hyrax abyssinicus;* after Brehm.

FIG. 3. Skeleton of the American mastodon; after Owen.

FIG. 4. Skull of Indian elephant sectioned longitudinally, showing the great development of air cells and the relatively small brain cavity; after Owen.
B, Cavity of brain; *i*, incisor (tusk); *m*, 3, 4, 5, molars 3, 4 and 5.

FIG. 5. *a*, Crown view, and *b*, longitudinal section of the molar tooth of an Indian elephant, schematic. Black, enamel; dotted portion, cement; cross-lined, dentine or ivory. Original.

FIG. 6. Section of skull of a very young and of a full-grown African elephant, showing the change of contour during growth due to the development of air cells or diploë. From Flower's Osteology, 1/4 and 1/12 natural size, respectively.

FIG. 7. Evolution of the Proboscidia. Original. Based upon restorations modeled by R. S. Lull.
a, *Elephas columbi;* *b*, *Mammut americanum;* *c*, *Tetrabelodon angustidens;* *d*, Palæomastodon; *e*, Mœritherium. Figs. *a*, *b* and *c* are 1/32, figs. *d* and *e* 1/16 natural size.

FIG. 8. Mammoth found frozen in the ice near Beresovka, Siberia, as it lay in the cliff, after Herz.

FIG. 9. The mammoth of Beresovka mounted in the St. Petersburg Zoölogical Museum; after Herz.

FIG. 10. Charging mammoth drawn on mammoth ivory by prehistoric man, after Lubbock.

FIG. 11. Prehistoric engraving of a mammoth, Cavern of Les Combarelles, Dordogne, France. 1/6, from MacCurdy; after Capitan and Breuil.

FIG. 12. Skull of Mœritherium; after Andrews. About 1/7 natural size.

FIG. 13. Last upper molar of Mœritherium. Drawn from a cast, No. 11663, Yale Museum, 1/2 natural size. Original.

FIG. 14. Skull of Palæomastodon; after Andrews. About 1/12 natural size.

FIG. 15. Last upper molar of Palæomastodon. Drawn from a cast, No. 11660, Yale Museum, 1/2 natural size. Original.

FIG. 16. Skull of *Tetrabelodon angustidens*. Original.

Fig. 17. Last upper molar, tooth of *Tetrabelodon angustidens*. Catalogue No. 11732 Yale Museum, 1/4 natural size. Original.
Fig. 18. Skull of *Dibelodon andium*, modified from Burmeister.
Fig. 19. Skull of *Mammut americanum*. Original.
Fig. 20. Last upper molar tooth of *Mammut americanum*. Catalogue No. 10681 Yale Museum, 1/4 natural size. Original.
Fig. 21. Restoration of the American mastodon, *Mammut americanum*, after Marsh, 1/32 natural size. The animal stands too high at the shoulders and the tusks are reversed, as they should curve inward at the tip. Catalogue No. 12600 Yale Museum.
Fig. 22. Molar tooth of *Stegodon clifti*. From a cast, No. 10759, Yale Museum, 1/4 natural size. Original.
Fig. 23. Molar tooth of *Elephas imperator*. Catalogue No. 11677, Yale Museum, 1/4 natural size. Original.
Fig. 24. Molar tooth of *Elephas columbi*. Catalogue No. 11683, 1/4 natural size. Original.
Fig. 25. Molar tooth of the mammoth *Elephas primigenius*; after Marsh.
Fig. 26. Mammoth found in the Lena Delta, Siberia, in 1799, as mounted in the St. Petersburg Zoölogical Museum. Portions of the hide still adhere to the head and feet; after Marsh.
Fig. 27. Jaw of Dinotherium, showing the downwardly directed lower tusks; after Kaup.